THE NEAR-BOTTOM CHLOROPHYLL A MAXIMUM IN ONSLOW BAY: EFFECTS OF WAVE EVENTS ON BENTHIC MICROALGAE RESUSPENSION

Gianluca Manes

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Approved by

Advisory Committee

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Chair

Accepted by

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Dean, Graduate School

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ABSTRACT

Both a significant benthic microflora and a near-bottom chlorophyll a maximum are present in Onslow Bay, NC. Over 80% of the chlorophyll a is associated with the sediments, supporting previous findings that primary production by microalgae on the continental shelf out to the shelf break is important. Benthic microalgae are likely to be the major producers in continental shelves like Onslow Bay where light flux to the bottom appears to be adequate to support them.

The existence of a near-bottom chlorophyll a maximum is due partly to resuspension by surface gravity waves. Orbital velocities and bottom shear stresses exceeded thresholds of 0.2-0.3 m/s and 0.2 N/m^2, respectively, and caused statistically significant increases in turbidity (NTU) and fluorescence (RFU). In addition to the magnitude of the orbital velocity measured by Turner SCUFA II *in situ* loggers the change in orbital velocity (or bottom shear stress) before and after a storm event, and the duration of the event also control the resuspension phenomena. However, other processes such as *in situ* growth of near-bottom microflora, sinking, and the spring bloom have to be considered as well in studying formation of near-bottom chlorophyll maxima.

I observed anomalously high values of turbidity and fluorescence at 1 m from the bottom in May-June 2002 and the lowest concentration of phytoplankton in the water column (near-bottom, mid-depth, surface) during this event. I hypothesize that demersal zooplankton moved into the water column at night and reentered the substrate by day and that holozooplankton were down in the water column near the bottom during the day and migrated upward at night. These migration patterns were responsible for the fluorescence and turbidity pattern. The high spikes in turbidity signals at 1 m were probably produced

by the high density of zooplankton (~$10^{4} m^{-2}$) and the fluorescence signal at 1 m was the result of their nocturnal feeding (the fluorescence signal was related to the chlorophyll a content in their guts).

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DEDICATION

I would like to dedicate this thesis to my grandparents, the ones whom I knew and the ones whom I did not have the opportunity to know. I deeply love you all.

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INTRODUCTION

Near-bottom chlorophyll a maxima have been observed frequently in studies of phytoplankton distributions in Onslow Bay. Paffenhöfer et al. (1980) measured chlorophyll a distribution in Onslow Bay in the summers of 1975 and 1976 and found near-bottom chlorophyll a maxima at a majority of their stations. Curtin (1979 a,b,c) conducted a study in November 1977, February 1978, and May 1978 and found near-bottom chlorophyll maxima at 17 of 29 stations, 12 of 30 stations, and 30 of 33 stations, respectively. Sinking of phytoplankton to the bottom in Onslow Bay is likely to be limited by physical processes, as Onslow Bay, like many continental shelves (as opposed to central gyre systems with deep chlorophyll maxima) is generally a physically dynamic environment (Cahoon 1990). Moreover, near-bottom chlorophyll maxima frequently corresponded with near-bottom particle concentration maxima, indicating that shade adaption is not an adequate explanation for the observed pigment distribution (Paffenhöfer et al. 1980).

It is likely that frequently observed near-bottom chlorophyll a maxima are created by resuspension of abundant benthic microalgae in this shelf ecosystem (Cahoon et al. 1990). The distribution, biomass, productivity, trophic significance, and taxonomic composition of benthic microalgae have been extensively studied in many estuarine, littoral and shallow subtidal habitats (e.g., Hustedt 1955, Round 1971, 1981, McIntire 1978, Admiral and Peletier 1980, Laws 1983, Lukatelich and McComb 1986, Sullivan and Moncreiff 1988, Cahoon 1999). Benthic microalgae are ecologically important. They can drive significant changes in vertical profiles of oxygen concentration, nutrient concentration, carbon dioxide-bicarbonate-carbonate concentration, pH, redox potential

across the sediment-water interface. Moreover they are important in terms of grazing interactions, supporting a broad diversity of organisms: bacteria, benthic protozoans including ciliates and foraminifera, herbivorous zooplankton, demersal and meiofaunal animals.

However, only a few studies have documented the taxonomic composition, distribution, biomass or even the existence of benthic diatom flora on the continental shelf or slope (Round 1971, McIntire and Moore 1977, Cahoon and Laws 1993, Cahoon 1999).

Cahoon et al. (1990) estimated that over 80% of the chlorophyll a in most of Onslow Bay is associated with the sediments. Photography of the sediments revealed extensive patches of microalgae firmly attached to the sediment. Light flux to the bottom appears to be adequate to support viable benthic microalgae at shallow slope depths (50-100 m) in Onslow Bay (Cahoon, 1992). Recent work suggests that primary production by microalgae on the continental shelf out to the shelf break is more important than previously thought (Cahoon and Cooke, 1992). Previous studies ignored benthic microalgae primary production and were focused only on water column phytoplankton biomass and primary production.

Benthic microalgae have been demonstrated to produce extracellular polymeric substances (EPS) that act to bind sediments (Decho 1990, Underwood et al. 1995). Benthic diatoms are major producers of this complex mix of polysaccharides and other compounds. This stabilization of the sediment is one factor likely to be responsible for maintenance of very high microalgal biomass levels at the sediment/water interface and resistance to resuspension.

Stabilization of the sediment offers several adaptive advantages to microalgae and is therefore likely to be a key feature of their ecology. It allows benthic microalgae to resist displacement and resuspension, which could carry them into less desirable habitats or expose them to suspension feeders. Stabilization reduces damage to microalgal cells by abrasion and collision with unconsolidated sediment grains (Delgado et al. 1991b, Miller 1989). It reduces resuspension of very fine-grained sediment particles and the light-limiting turbidity that might then result (Roemer et al. 1984). Stabilization can be overcome by sufficient physical force, leading to resuspension of benthic microalgal biomass.

Water motions in the southeastern United States continental shelf (commonly called the South Atlantic Bight) are caused by numerous physical processes. Synoptic (two days to two weeks) and seasonal (periods of one year) scale motions occur in response to direct forcing by winds (synoptic scale) and variations in thermohaline inputs (seasonal scales). Synoptic variability occurs predominantly over the time scale of the cyclonic and anticyclonic perturbations of the wind field (Pietrafesa 1978). Other low frequency fluctuations occur in response to external forcing from the deep ocean, e.g., eddies and Gulf Stream intrusions.

At higher frequencies, the astronomically forced semidiurnal tides propagating shoreward from the deep ocean are a dominant feature. Between these semidiurnal tides and the lower frequency weather continuum three processes occur in varying degrees across the shelf: diurnal tides, inertial oscillations, and sea breeze. These all have time scales of roughly one day. Processes occurring at frequencies higher than the semi-diurnal tides, such as internal-gravity waves, and surface gravity waves, together with

lower frequency processes, may supply sufficient force to resuspend benthic microalgae. Onslow Bay is a suitable environment in which to study the distribution of benthic chlorophyll a at and near the sediment-water interface because of the frequency of storms, limited sediment input (Riggs et al. 1996), observations of fairly ubiquitous near-bottom chlorophyll maxima.

The objective of this study was to test hypotheses concerning resuspension of benthic microalgae and formation of near-bottom chlorophyll maxima in Onslow Bay:

1) Near-bottom turbidity and fluorescence increase significantly only when near-bottom orbital velocity and bed shear stress increase significantly.

If surface gravity waves do not always create near-bottom chlorophyll a maxima, other causal factors or cofactors have to be considered: a) accumulation of phytoplankton settling out of the water column at depths with light flux adequate to support growth; b) *in situ* growth by near-bottom microflora; 3) advection of chlorophyll a rich water (e.g., outwelling from estuaries). However only the wave effects hypothesis was tested directly in this study. When this hypothesis did not explain the near-bottom chlorophyll maximum the other explanations were invoked considering the overall set of data and the previous literature.

METHODS AND MATERIALS

Onslow Bay is a portion of the North Carolina continental shelf bounded by Cape Lookout shoals (34.6° N, 76.5° W) on the northeast side to Frying Pan Shoals (33.8° N 78 W°) on the southeast side (Fig. 1). The Bay is approximately 80 to 110 km wide and the shelf break is at approximately 55 m depth.

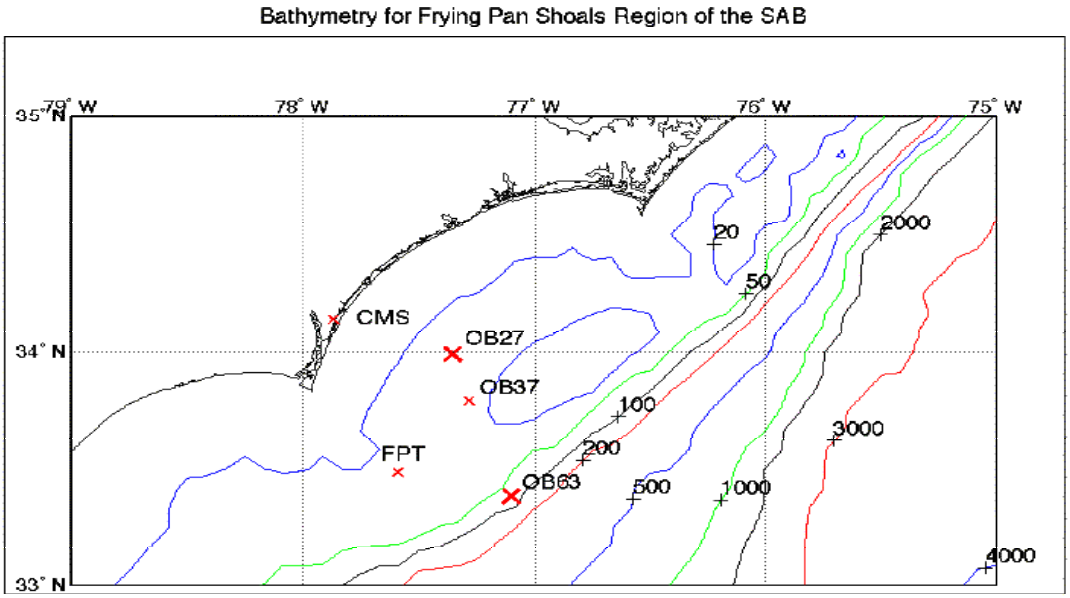

Fig.1.Bathymetric map of Onslow Bay, North Carolina coastline, including OB27.

To investigate the resuspension of chlorophyll a, two underwater fluorescence/turbidity loggers were mounted on a 2 meter "quadpod" frame at the OB27 site (33° 59 N, 77° 21 W, 28 m depth). Near-bottom particle density measurements were obtained through the use of two underwater SCUFA II loggers, fitted with copper antifouling screens, recording fluorescence at 1 m and at 2.4 m from the seabed every 10 minutes in Onslow Bay during the period October 30, 2001, to June 14, 2002 (during the course of 4 deployments). In addition to the fluorescence sensor, there was a turbidity

sensor, which measured turbidity through 90^0 light scatter. An Ultra-Bright LED was used as the excitation light source (Excitation = 460 nm peak, 30 nm bandwidth and Emission = 685nm peak, 30 nm bandwith), and optical filters were used on both excitation and emission channels to allow only the wavelengths of interest to pass. Turbidity was measured in Nephelometric Turbidity Units (NTU) and fluorescence in Relative Fluorescence Units (RFU). Turbidity and fluorescence data were recorded simultaneously allowing comparisons. Water column samples for analysis of phytoplankton biomass and sediment samples for analysis of benthic microalgae biomass were collected at OB27, during a series of research cruises during the period April 18, 2000 to December 8, 2002. Water column samples were collected at surface, middle and bottom depths by a CTD/Rosette sampler. Sediment samples (3-4 cm deep) were collected by SCUBA divers, using 2.5 cm core tubes.

Chlorophyll a in sediment was determined by the method of Whitney and Darley (1979), which employs partitioning of acetone pigment extracts with hexane followed by spectrophotometric measurement, to quantify chlorophyll a without interference from degradation products that are soluble in acetone. Water column chlorophyll was determined fluorometrically according to Welschmeyer, 1994.

SCUFA II fluorescence/turbidity loggers were deployed at OB27 by divers who attached units to the "quadpod" at 1 m and 2.4 m from the bottom. The units were deployed during the periods October 31, 2001 to December 6, 2001, December 7, 2001 to February 21, 2002, March 5, 2002 to April 4, 2002 and May 4, 2002 to June 14, 2002.

Values of turbidity and fluorescence from both SCUFAs were plotted using MATLAB software (the time data were referenced to Greenwich Meridian Time). The

numeric data sets were preprocessed by removing occasional instrument-caused outliers, and missing values, which were always single point values. These outliers were identified as points occurring when the difference absolute value between successive values was greater than three times the standard deviation for the whole data set.

Surface wave data obtained from Frying Pan Shoal Tower "FPSN7" (Fig. 1) (http://www.ndbc.noaa.gov/station_page.phtml?$station=fpsn7) were used to calculate the effects of surface wave heights and periods on near-bottom physical processes. Average wave period (*T)* defined as the average period of all waves during a 20 minute period per hour, and significant wave heights (*H)*, defined as the average of the highest one third of all the wave heights during the same 20 minute sampling period per hour, were reported by National Data Buoy Center.

To better understand the relationship among fluorescence, turbidity and physical processes, the orbital velocity (u_b) and bed shear stress (τ_c) were calculated and plotted with MATLAB. The normal expression for bed shear stress in steady flow is, from elementary fluid mechanics (Von Karman 1930):

1) $$\tau_c = \rho g\left(\frac{V^2}{C^2}\right)$$

τ_c is the constant bottom shear stress acting against the flow

C is the Chezy friction factor $C = 18\log\frac{12h}{r}$

r is roughness of the bottom, $r = 2.5D_{50}$

D_{50} is mean diameter of the sediment

h is water depth

g is the acceleration of gravity

V is the current velocity averaged over the flow cross section

ρ is the density of the fluid

However, this study examines the effects of oscillating flows driven by wave action. Jonsson (1975) carried out experiments to determine bed shear stresses under waves and found that this shear stress, τ_w, could be described by

2) $$\tau_w = \frac{1}{2} f_w \rho u_b^2$$

where f_w is a dimensionless coefficient, u_b is the instantaneous water velocity near the bottom.

Jonsson derived an empirical relation for f_w in terms of readily measurable parameters: the bottom roughness, *r*, and the amplitude of the water displacement near the bottom, a_b. His relationship as rewritten by Swart (1974) is:

3) $$f_w = \exp\left[-5.977 + 5.213\left(\frac{a_b}{r}\right)^{-0.194}\right]$$

This relation is only valid for $1.47 < \frac{a_b}{r} < 3000$. For values of $\frac{a_b}{r} \le 1.47$, f_w has constant value of 0.32.

Both u_b and a_b are easily evaluated using linear wave theory. The velocity at the bottom, u_b is:

4) $$u_b = \frac{\omega H}{2} \frac{1}{\sinh(kh)}$$

Similarly a_b

5) $$a_b = \frac{H}{2} \cdot \frac{1}{\sinh(kh)}$$

ω is wave frequency $\left(\frac{2\pi}{T}\right)$

k is wave number $\left(\frac{2\pi}{\lambda}\right)$

H is significant wave height

The computation of u_b and a_b just above neglect boundary layer effects.

In order to calculate the orbital velocity (u_b), the wave length (λ) had to be derived using Pade`s recursive method (Kraus 1981):

6) $$F = Y + \frac{1}{1 + 0.6522 \cdot Y + 0.4622 \cdot Y^2 + 0.0864 \cdot Y^3 + 0.0675 \cdot Y^4}$$

where F is a parameter depending on Y

7) $$Y = \omega^2 \cdot \frac{h}{g}$$

and

8) $$k = \frac{2\pi}{\lambda} = \omega \sqrt{\frac{F}{gh}} \Rightarrow \lambda = \frac{2\pi}{\omega} \cdot \left(\frac{F}{gh}\right)^{-0.5}$$

λ is wavelength

The wavelength values (found using the Pade's method) were then used to calculate orbital velocity values (equation 4) and bed shear stress values (equation 2). Knowing the wavelength, one can derive the wave number (2π/λ), and calculate the orbital velocity since the wave frequency (ω), a function of the wave period (obtained from Frying Shoals data), the wave height (obtained from Frying Pan shoals data) and the water depth in Onslow Bay (at OB27) were known.

Knowing the orbital velocity and calculating a_b (equation 5), a function of the wave number, and estimating the bottom roughness (r) through the empirical formula (Nielson 1979).

9) $$r = 2.5 \cdot D_{50}$$

the bed shear stress values were obtained.

Next, the fluorescence, turbidity, orbital velocity, and bed shear stress from all four deployments were plotted together to examine results from the SCUFAs at 1 meter and at 2.4 meters above the bottom during the entire sampling period (looking for maximum and minimum values) to examine depth-related differences in these parameters (Fig.2). The last of these deployments, (May 4, 2002, to June 14, 2002), because of the anomalous signal from the SCUFA II at 1 m, was considered separately.

I examined the effects of wave action on near-bottom fluorescence and turbidity values by inspecting the wave-derived orbital velocity data for times when orbital velocity values increased sharply (to more than 0.2 m/s) within 1-2 days in order to examine the effects of the greatest wave events (Fig. 3). I then used one-way analysis of variance (1-way ANOVA) of the orbital velocity data for periods of similar duration before and after the observed increases to determine if the differences in mean orbital velocity values were significantly different ($p<0.05$). If the differences in mean orbital velocity values were significant, thus defining an "orbital velocity event", I used 1-way ANOVA to determine if significant increases in fluorescence and turbidity values for the same "before" and "after" periods had also occurred when orbital velocity values increased.

I defined "fluorescence events" similarly by inspecting the data for times when fluorescence values increased sharply within a period of 1-2 days, then using 1-way ANOVA to determine if the mean values of fluorescence in periods of similar duration before and immediately after the increase occurred were significantly different. If this difference was significant ($p<0.05$), I then compared mean values of orbital velocity for the same "before" and "after" periods using one-way analysis of variance to determine if these differences were significant.

RESULTS

Benthic microalgal biomass, measured as chlorophyll a, consistently exceeded depth-integrated water column chlorophyll a. Benthic microalgal biomass calculated from core samples during September and December 2001 and February, April, May, and June 2002 (Table 1) was compared with chlorophyll a data from the CORMP project (Table 2) sampled from April 18, 2000, to December 8, 2002, at OB27 (28 m depth). Benthic microalgal biomass ranged from 32.6 to 50.4 mg Chl a/m^2 with a mean of 45.7 mg Chl a/m^2. This value was consistently higher than the integrated water column biomass, with a mean of 4.04 mg Chl a/m^2 (or 9.17 % of the total Chl a /m^2). Average near-bottom chlorophyll a sampled from April 18, 2000, to December 8, 2002, at OB27 was 0.227 mg Chl a/m^3, greater than surface and mid-column values of 0.100 and 0.106 mg Chl a/m^3.

Hourly averaged fluorescence (RFU) and turbidity (NTU) data from the SCUFA II units deployed at OB27 displayed several notable patterns during the deployment periods, October 2001 to June 2002 (Fig. 2). Fluorescence and turbidity values from the SCUFA II at 1 m were generally higher in October and November (4-4.5 RFU and 6-7 NTU) than in the period December to January (2-3 RFU and ~2 NTU). Fluorescence and

turbidity values recorded by the SCUFA II at 1 m from the bottom were also generally higher than values recorded by the SCUFA II at 2.4 m during October and November, but more similar during December to February. An overall increase in fluorescence and turbidity values was recorded by both SCUFAs during March and April, with the SCUFA II at 2.4 m recording higher values than the SCUFA II at 1 m from the bottom. A very different and anomalous pattern that was observed during the period May-June 2002 is presented and analyzed separately.

Wave data from Frying Pan Tower (significant wave heights and dominant wave periods) and values of resulting near-bottom orbital velocities and bottom shear stress were plotted for the period October 2001 to June 2002 (Fig. 3). These plots illustrate the ranges of these observed and calculated values. There were several storm events discernible in this data set, but no major storms (tropical or extratropical cyclones) occurred during this period.

The relationships between wave events, quantified as times of elevated values of calculated orbital velocity and bed shear stress, and near-bottom fluorescence and turbidity were initially examined by plotting the respective data sets for the sampling periods between October 2001 and April 2002 (Fig. 4). Initial inspection of the data sets revealed several instances when spikes in near-bottom orbital velocity and bed shear stress appeared to correspond closely with increases in near-bottom fluorescence and turbidity, here termed “orbital velocity events”. However, some increases in near-bottom fluorescence and turbidity appeared unrelated to changes in near-bottom orbital velocity and bed shear stress (here termed “fluorescence events”). Finally, relatively large

increases in near-bottom fluorescence and turbidity during a longer period in March-April 2002 did not appear to correspond to any changes in near-bottom orbital velocity.

Considering the whole data set of physical and biological variables (turbidity, fluorescence, orbital velocity, and bed shear stress) five "orbital velocity" events were identified as having high orbital velocity (≥ 0.2 m/s) or bed shear stress (≥ 0.2 N/m^2) and two "fluorescence events" and one longer period as having high fluorescence (fluorescence >2 RFU). An orbital velocity "event" was defined as a period of significantly higher values of orbital velocity and consequently higher bed shear stress (Table 3) compared to "before event" values. For each event, mean orbital velocity, mean fluorescence, and mean turbidity were calculated over 6-10 days periods (with the exception of a longer, distinct period for which the means were calculated over a longer duration). In order to analyze biological factors and physical factors potentially causing the near-bottom fluorescence maximum the mean orbital velocity was used as a criterion to order the events and the longer period in sequence from the lowest (0.03 m/s) to the highest value (0.16 m/s) (Table 3). The highest mean values of orbital velocity occurred during the November- January period (Table 3).

Looking at the overall data set from October 31, 2001 to April 4, 2002, a sharp increase in fluorescence and turbidity data values during March 5, 2002-April 4, 2002 stands out. The SCUFA II at 2.4 m from the bottom showed higher values in fluorescence and turbidity than the SCUFA II at 1 m. During this month, the results indicated an unusual pattern since, during the period October 31, 2001-December 6, 2001, the data set showed lower values in fluorescence and turbidity from the SCUFA II at 2.4 m compared to the SCUFA II at 1 m and comparable values during the period December 7, 2001-

February 21, 2002 (Fig. 2). Examining the orbital velocity and bed shear stress data there is no evidence that supports wave action as the cause of significant increases in fluorescence and turbidity values during March-April. This represented a calm period with a lack of storms (Tables 3 and 4). Considering this and the previous literature (Cahoon and Laws 1993, Cahoon 1992, Cahoon 1999) about this environment, the results are consistent with a spring bloom of phytoplankton taking place during this period of time.

The "fluorescence events" were defined as periods of significantly higher values of fluorescence (and turbidity) compared to "before event" values. Two "fluorescence events" have been identified in the overall data set as increases in fluorescence (Fig. 5-6) that did not correspond to any significant change in the orbital velocity and bed shear stress (Fig. 3). During the periods December 8, 2001-December 15, 2001 and November 1, 2001-November 10, 2001, there was no wave driven forcing of these "events". Statistical analyses of the orbital velocity values during the "event" versus "before the event" periods showed that orbital velocity either did not change significantly (December) or was significantly lower during the "event" compared to "before event" (November). Other explanations aside from wave action have to be considered to explain these increases in the fluorescence signal from the SCUFA II.

Inspection of the data set revealed that there were short periods (<2 days) when wave action went up noticeably, and that appeared to correspond to fluorescence increases (Fig. 7-11). Subsequent analyses of the orbital velocity data, fluorescence data, and turbidity data showed that there were five cases in which there was a significant increase in those properties in the same time frame (Table 4). The inference was that

wave action exerted bed shear stress sufficient to cause resuspension of the microalgae into the water. The average fluorescence increase in the orbital velocity events was 30.6 %, and the values of the near-bottom phytoplankton, mid-depth, and surface biomass sampled from April 18, 2000 to December 8, 2002 (CORMP) were respectively 0.227, and 0.106, and 0.100 mg Chl a/m^3. If wave-induced resuspension of microalgae is responsible for the observed increases in fluorescence, then some but not all of the near-bottom chlorophyll a maximum is caused by wave action at the bottom. It is not possible to rule out the possibility that other processes are taking place together with wave action, processes that could potentially contribute to create the near-bottom maximum observed.

The May-June data set showed a completely different pattern in near-bottom turbidity and fluorescence (Fig. 12). The data showed a distinctly diurnal pattern from May 10 to May 22 (Fig. 13) with anomalously high values of turbidity. Spikes in fluorescence and turbidity occurred from 00 to 9 am (GMT), respectively, corresponding to 8 p.m. to 5 a.m. Eastern time (approximately sunset and sunrise hours) (Fig. 14, May 12, 2002-May 13, 2002). The fluorescence signal magnitude was in the same range as fluorescence values found in the previous deployments but the turbidity signal showed much higher values, most of the time higher than 20 NTU with spikes reaching values of over 70 NTU. This pattern in May-June was probably related to vertical migrations by demersal zooplankton, whose population may have grown in response to the spring bloom in March-April. A SCUFA II instrument immersed in preserved demersal zooplankton water samples yielded similarly high turbidity values in a laboratory experiment.

DISCUSSION

The results of this study confirmed the existence of both a significant benthic microflora in Onslow Bay and a near-bottom chlorophyll a maximum at OB27. Sediment chlorophyll a concentrations ranged between 32 and 50.4 mg Chl a /m^2 (Table 1) with a mean of 45.7 mg Chl a /m^2, versus integrated water column Chl a of 4.0 mg/m^2, supporting previous findings that over 80 % of the chlorophyll a in Onslow Bay is in the sediments (Cahoon et al. 1990). The existence of a near-bottom chlorophyll maximum at OB27 (an average of 0.227 mg Chl a /m^3 vs mean mid-column value of 0.100 and surface value of 0.106 mg Chl a /m^3; Table 2) is a frequent and widespread feature of this continental shelf environment (Paffenhöfer et al. 1980, Curtin 1979 a,b,c, Cahoon et al. 1990).

The existence of a near-bottom chlorophyll a maximum and the relatively large amount of chlorophyll a in the sediment is unlikely to be the result of sinking phytoplankton alone for several reasons. An average of four times as much chlorophyll a has been found in the sediment as in the entire overlying water column (Table 1; Cahoon et al. 1990). Light flux to the bottom appears to be adequate to support viable benthic microalgae at shallow slope depths (50-100 m) in Onslow Bay (Cahoon, 1992). Grazing in the water column likely limits the amount of phytoplankton that could sink to accumulate in the sediments. Much of the phytoplankton produced in the continental shelf waters is exported (Yoder 1985), limiting accumulation in the near-bottom zone. Shade adaption, an increase in chlorophyll a content per cell in this case, is not an adequate explanation for the observed pigment distribution. This is because near-bottom particle maxima occurred coincidently with near-bottom chlorophyll a maxima in earlier

studies (Paffenhöfer et al. 1980). Finally, rapid accumulation of phytoplankton pigments in the sediments caused by grazing and excretion of fecal pellets that sink rapidly cannot explain the chlorophyll a concentration at the bottom. This is due to the fact that virtually all the pigment in fecal matter is degraded, not intact chlorophyll a (Shuman and Lorenzen 1975), as measured by the technique of Whitney and Darley (1979) used in this study. Onslow Bay, like many continental shelves is a physically dynamic environment (Cahoon 1990). Frequently wind-storms induce waves that scour the bottom, creating high orbital velocities and high bed shear stress, in addition to other processes. Onslow Bay is not considered a depositional environment because of a lack of sediment source (Riggs et al. 1997).

Waves likely play an important role in the distribution of primary producers in Onslow Bay by suspending benthic microalgae. Wave-stresses frequently caused the presence of near-bottom chlorophyll a maxima in Onslow Bay due to the resuspension of sediment-associated microalgae. However, considering the previous literature (Cahoon et al. 1990, Cahoon and Cooke, 1992) three other processes, *in situ* production (December 8 December 15, 2001 and November 1 November 10, 2001) the spring phytoplankton bloom in March-April (potential causes of near bottom chlorophyll a) and vertical migration by demersal and holozooplankton in May-June (not a potential cause of near bottom chlorophyll a) may have created patterns in the SCUFA II data that could not be explained by wave effects.

Results of this study indicated that near-bottom velocities in the range of 0.2-0.3 m/s and bed shear stress values of approximately 0.2 N/m^2 were sufficient to cause significant increases in fluorescence and turbidity consistent with resuspension of benthic

microalgae. Similar results have been found in other studies dealing with sediment resuspension. Wood and Widdows (2002) found critical erosion velocities between 0.15 and 0.31 m/s in an intertidal transect. During the field deployments of a flume in the Humber estuary (U.K.), Austen et al. (1999) investigated the erodibility of mudflat surfaces in the Lister Dyb tidal area (Wadden Sea). They observed that the erosion threshold was mainly controlled by the relationship between algal biomass, expressed as chlorophyll a content, and the abundance of deposit feeders. The threshold speed at which sediment erosion starts was taken as a linear function of surface chlorophyll a concentration (this was supported by the experiments of Sutherland et al. 1988). A mean erosion threshold of 0.2 N/m^2 was found at one of their stations. Although the comparability of intertidal and subtidal properties remains to be evaluated, the ability of intertidal flow to suspend sediments strongly supports the argument that subtidal flows of similar magnitude can suspend benthic microalgae.

Turbidity and fluorescence increased significantly in response to increases in mean orbital velocity during November 15, 2001-November 21, 2001 (Fig. 8) and December 24, 2001-December 27, 2001 (Fig. 7). However the magnitude in mean orbital velocity was relatively low in comparisons to other times when significant increases in turbidity and fluorescence were apparently caused by much greater increases in orbital velocity (Table 3). This suggests that the change in orbital velocity necessary to cause a significant increase in fluorescence and turbidity may be controlled by other factors having to do with the resistance to erosion of the bottom sediment. In addition, sediment stabilization is affected by algal biomass (important for sediment stabilization due to their production of extracellular polymeric substances), abundance of deposit feeders, surface

sediment type, water content of the bed material (Austen et al. 1999), and/or intensity of sediment surface reworking, microphytobenthos assemblage composition, and endobenthic macrofauna present (Riethmueller et al. 2000). Resuspension of microalgae and sediment erodibility in Onslow Bay seemed, nevertheless, more dependent on physical processes. More important than the magnitude of the mean orbital velocity by itself, I think the magnitude of change in orbital velocity controls the resuspension phenomena. The previous events (November and December 2001) had a 3x and 4.6x increase in mean orbital velocity. It is likely, too, that Chl a and sediment stabilization are related during winter months. When the growing season is over, the sediments are less resistant to erosion, and resuspension of microalgae can occur at relatively low current speeds.

The January (Fig. 9) and February (Fig. 10) events and November 27, 2001-November 30, 2001 (Fig. 11) event represented the highest energy events. Their mean orbital velocities were 0.130, 0.133, 0.16 m/s, respectively, but they still did not represent high energy phenomena if mean magnitude is considered. However, the maximum values of the orbital velocity and bottom shear stress for these three events, respectively, 0.56 m/s (bottom shear stress = 1.29 N/m^2), 0.35 m/s (bottom shear stress = 0.55 N/m^2) and 0.28 m/s (bottom shear stress = 0.37 N/m^2), where much higher than maximum orbital velocity values during preceding "events" (0.10 m/s for November 15, 2001-November 21, 2001, and 0.20 m/s for December 24, 2001-December 27, 2001). During the January event there was a 4.3-fold increase in mean orbital velocity; 4.4-fold times increase in the February event; and a 6-fold increase during the November 27, 2001-November 30, 2001 event. This last event had a maximum orbital velocity of 0.28 m/s, which was lower than

the maximum orbital velocity in January and February, but had the highest mean orbital velocity (0.16 m/s). This is due to the fact that for almost two days the orbital velocity was greater than 0.2 m/s, meaning that the duration of the event is also a significant variable controlling the resuspension phenomenon. High significant wave heights continued for 32 hours during both January and February events. During November 27-November 30, 2001 high wave periods continued for 63 hours. It is important to acknowledge that orbital velocity is a function of both wave period (or wave length) and wave height. In fact during January and February high mean orbital velocity was due to high wave heights (2-4.97 m), but during the November "event" wave heights were low (1.05-2 m) and long wave periods (7.27-9.04 s) determined the observed high mean orbital velocity.

The January event had the highest mean fluorescence and the two events in February 1-February 9, 2001 and November 27-November 30, 2001 had low values of fluorescence but high values of turbidity. This suggests that the amount of detrital material eroded was relatively high, but the content of chlorophyll a in it was relatively low during November and February.

Another potential contribution to the near-bottom chlorophyll a maximum could be *in situ* growth of near-bottom microflora. During the period November 6, 2001-November 10, 2001 (Fig. 6) the mean value of orbital velocity (0.035 m/s) was significantly lower compared with the period before the event (0.049 m/s). Similarly, during the December 12, 2001 December 15, 2001 event (Fig. 5), there was no significant difference in the mean orbital velocities during the event period (0.035 m/s) compared with the period before the event (0.033 m/s). Increases in fluorescence and turbidity,

however, occurred during the "event" periods (the rate of growth μ per day was 0.122 over this period). The hypothesis of *in situ* production is also supported by the fact that light extinction studies (Schneider 1976, Cahoon 1987, Cahoon 1999) indicate that light flux to the bottom in this area frequently exceeds the 1% level commonly thought to delimit the euphotic zone. Nutrients are likely to be concentrated (because of macrofauna excretion and frequent intrusion of slope water along the bottom, Cahoon 1999) at the sediment water interface and released from the sediments (Rowe et al. 1975). However, it is not possible to reject the sinking hypothesis because low orbital velocities allow sinking and accumulation as well.

The March 5, 2002 to April 4, 2002 period (Fig. 4) likely represented a classical example of the annual spring bloom. The data showed a relatively high value of mean fluorescence (3.23) with the highest maximum fluorescence value of 5.9, and the highest mean turbidity (5.37 NTU). The concentration of chlorophyll a in the column water increased markedly, as indicated by both SCUFAs' fluorescence responses (Fig. 2). The hypothesis of the spring bloom was also supported by the fact that values from the SCUFA II at 2.4 m were generally lower than the values from the SCUFA II at 1 m during October and November, not different from each other during December to February but higher during March and April (Fig. 2). The results suggested that the higher values of fluorescence and turbidity at 1 m during October and November may be phenomena of resuspension caused by physical forces (higher significant wave height, orbital velocity and bottom shear stress). By contrast, the higher values of fluorescence and turbidity at 2.4 m during March-April may be related to a bloom of near-bottom benthic microalgae and water column phytoplankton. Thus, the phytoplankton blooms

may be relatively important in creating a near-bottom chlorophyll a maximum during at least a portion of the year, while resuspension of benthic microalgae is more important at other times.

The SCUFA II data set from May-June 2002 differed quantitatively from the previous data sets and appears related to vertical migration by holozooplankton and/or demersal zooplankton. Demersal zooplankton are distinguished from zooplankton that remain in the water column continuously by their periodic association with benthic substrates (Alldredge and King 1977, Porter and Porter 1977, Robichaux et al. 1981, Cahoon and Tronzo 1992). Demersal zooplankton in Onslow Bay are approximately as abundant as holozooplankton, $\sim 10^4$ m^{-2} (Cahoon 1992). Estimates of demersal zooplankton abundance in Onslow Bay are generally higher than those reported from other habitats (Cahoon and Tronzo 1992). I hypothesize that demersal zooplankton moved into the water column at night and reentered the substrate by day and that this migration pattern was responsible for the fluorescence and turbidity patterns. The high spikes in turbidity signals at 1 m were probably produced by the high density of zooplankton. The fluorescence signal at 1 m was likely the result of their nocturnal feeding (and the resulting increased chlorophyll content in their guts). These data also suggested high concentrations of zooplankton following the phytoplankton bloom in March-April 2002. The concentration of phytoplankton in the water column (near-bottom, mid-depth, surface) in June 2002 is the lowest of the year, perhaps due to zooplankton grazers that bloomed in May-June 2002.

CONCLUSION

Continental shelves and other neritic ecosystems represent a relatively small but ecologically important proportion of the total area of the oceans. Benthic microalgae are likely to be the major primary producers in continental shelves like Onslow Bay, where their biomass equals or exceeds that of phytoplankton. Benthic microalgae seem to be especially important primary producers in the broad mid-shelf region (10-40 m). In this region water depth and clarity permit the highest relative light flux to the bottom and sediment chlorophyll a is consequently much greater than integrated water column chlorophyll a.

This research indicates that storm waves in Onslow Bay are often responsible for the observed near-bottom chlorophyll a maximum via resuspension. However, other processes such as the spring bloom, in *situ* production, and sinking must also be considered in studying formation of frequent and widespread near-bottom chlorophyll a maxima in this continental shelf ecosystem.

PRIMARY FINDINGS

1) Evidence that wave action contributes to formation of frequent chlorophyll a maxima but
2) Others factors contribute to formation of near-bottom chloropyll a maxima in Onslow Bay
3) This is first documented record of spring phytoplankton bloom in Onslow Bay
4) The *in situ* instrumentation also detected a bloom of and vertical migration by demersal zooplankton

Table 1. Mean and standard deviation values of chlorophyll a measured in replicate sediment core samples for benthic microalgal biomass with the method of Whitney and Darley (1979) during September, December 2001 and February, April, May, June 2002.

Date	Mean (mg Chl a/m^2)	Std dev	n
9/24/01	48.08	4.79	8
11/8/01	32.64	8.41	8
2/2/02	44.80	35.66	14
4/2/02	48.17	9.84	16
5/2/02	50.45	9.84	16
6/2/02	50.45	32.76	16

Table 2. Mean and standard deviation of phytoplankton biomass (mg chl a/m^3) sampled from April 18, 2000 to December 8, 2002 (Coastal Ocean Research Monitoring Program).

Depth at OB27	Mean (mg Chl a /m^3)	Std dev	n
Surface	0.100	0.073	17
Mid-depth	0.106	0.084	18
Near-Bottom	0.227	0.184	18

Table 3. Comparisons of mean values of orbital velocity (calculated from Frying Pan Shoals data), fluorescence, and turbidity (from SCUFA II deployments at OB27) for "Event " and "Before Event" periods, October 2001-June 2002. "Events" were defined as periods of either significantly higher values of fluorescence and turbidity or orbital velocity (indicated in bold). In the one way analysis of variance "p" values associated with the F ratio are designated as follows: ns= p>0.05 (non significant), '*'= p <0.001 or less.

	Mean Orbital Velocity m/s	Mean Fluorescence	Mean Turbidity NTU
Event 3/5/02- 4/4/02	0.03*	**3.23***	**5.37***
Before Event 10/30/01-2/21/02	0.04	1.85	2.30
Event 12/12/01-12/15/01	0.035ns	**2.37***	**1.61***
Before Event 12/8/01-12/11/01	0.033	1.45	1.35
Event 11/6/01-11/10/01	0.035*	**2.39***	**2.17***
Before Event 11/1/01-11/5/01	0.049	2.03	1.78
Event 12/24/01-12/27/01	**0.042***	2.34*	1.80*
Before Event 12/20/01-12/23/01	0.009	1.88	1.58
Event 11/15/01-11/21/01	**0.06***	2.18*	2.93*
Before Event 11/10/01-11/15/01	0.02	1.73	2.14
Event 1/7/02-1/9/02	**0.13***	3.80*	4.31*
Before Event 1/1/02-1/3/02	0.03	2.1	2.52
Event 2/7/02-2/9/02	**0.131***	1.43*	2.97*
Before Event 2/1/02-2/3/02	0.03	0.76	1.89
Event 11/27/01-11/30/01	**0.16***	1.94*	2.88*
Before Event 11/23/01-11/26/01	0.026	1.53	2.38

Table 4. Results of comparisons of orbital velocities, fluorescence, and turbidity values between defined periods, using 1-way ANOVA.

		1-way ANOVA results		
Time Comparisons	Dates	Orbital velocity (m/s)	Fluorescence (RFU)	Turbidity (NTU)
Spring bloom period	3/5/02-4/4/02	p<0.0009	p<0.0001	p<0.0001
Winter period	10/30/01-2/21/02	F=11.03, df 1,3455	F=7807.99, df 1,3226	F=2114.24, df 1,3223
Fluorescence events				
Event	12/12/01-12/15/01	p>0.05	p<0.0001	p<0.0001
Non event	12/8/01-12/11/01/	F=0.41, df 1,140	F=662.62, df 1,140	F=375.51, df 1,140
Event	11/6/01-11/10/01	p<0.0005	p<0.0001	p<0.0001
Non event	11/1/01-11/5/01	F=12.48, df 1,188	F=7807.99, df 1,188	F=1280.96, df 1,188
Orbital velocity events				
Event	12/24/01-12/27/01	p<0.0001	p<0.0001	p<0.0001
Non event	12/20/01-12/23/01	F=34.31, df 1,140	F=120.49, df 1,140	F=381.23, df 1,140
Event	11/15/01-11/21/01	p<0.0001	p<0.0001	p<0.0001
Non event	11/10/01-11/15/01	F=104.60, df 1,260	F=7807.99, df 1,260	F=610.09, df 1.258
Event	1/7/02-1/9/02	p<0.0001	p<0.0009	p<0.0009
Non event	1/1/02-1/3/02	F=27.27, df 1,92	F=5009.74, df 1,92	F=620.89, df 1,258
Event	2/7/02-2/9/02	p<0.0001	p<0.0009	p<0.0009
Non event	2/2/02-2/9/02	F=16.91, df 1,92	F=27.27, df 1,92	F=185.85, df 1,92
Event	11/27/01-11/30/01	p<0.0001	p<0.0001	p<0.0009
Non event	11/23/01-11/26/01	F=318.19, df 1,140	F=260.93, df 1,140	F=381.04, df 1,140

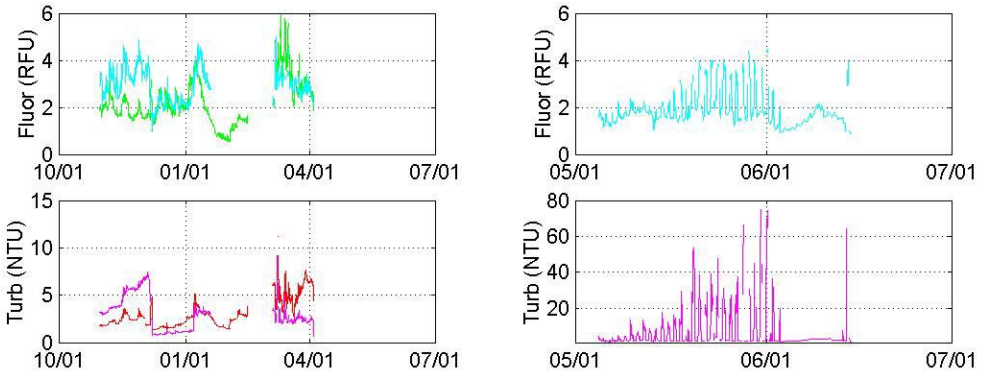

Fig. 2. Plots of averaged hourly fluorescence (Relative Fluorescence Units, RFU) and turbidity (Nephelometric Turbidity Units, NTU) data from SCUFA II at 1m (light blue and magenta) and SCUFA II at 2.4 m (green and red) at OB27 vs. mo/day from October 30, 2001 to April 4, 2002. The May-June data set showed fluorescence signal magnitude in the same range as fluorescence found in previous period but turbidity signal showed much higher values.

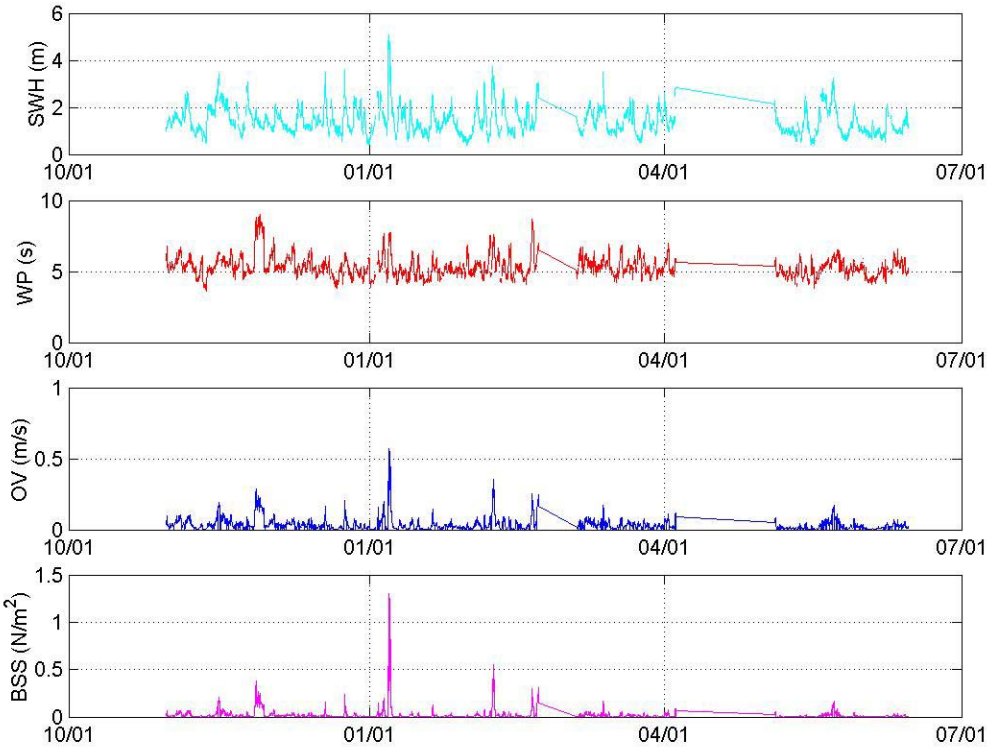

Fig.3. Plots of averaged hourly significant wave height (SWH, m) and wave period (WP, s) data from Frying Pan Shoals Tower and derived values of orbital velocity (OV, m) and bed shear stress (BSS, N/m^2) vs. mo/day from October 30, 2001 to June 14, 2002.

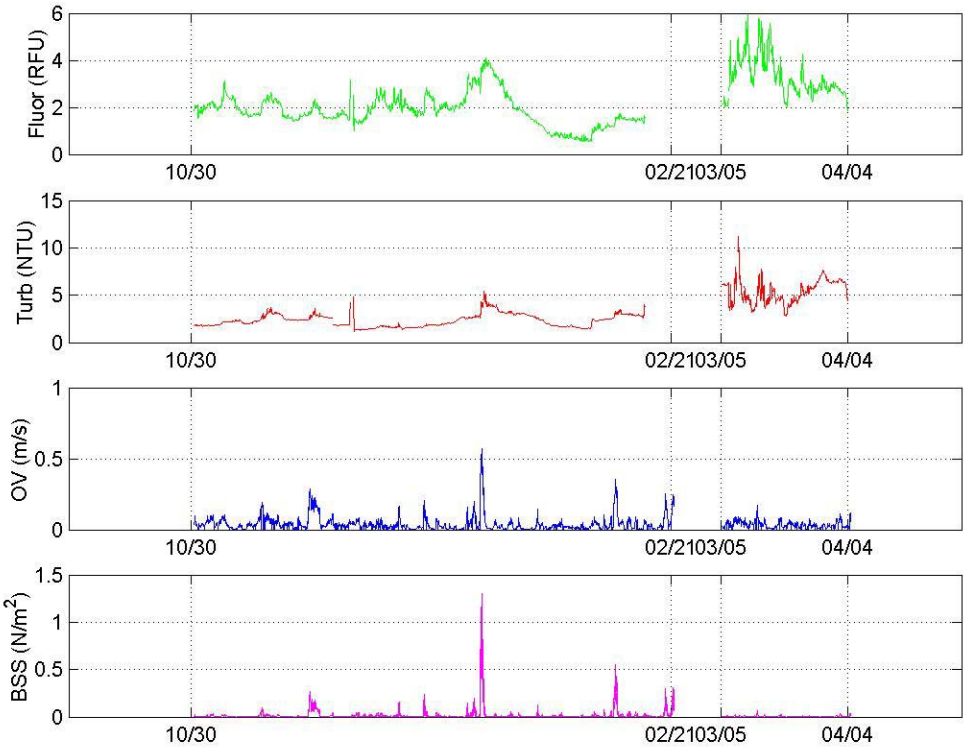

Fig.4. Plots of averaged hourly fluorescence (Fluor, RFU), turbidity (Turb, NTU), orbital velocity (OV, m/s) and bed shear stress (BSS, N/m^2) data for the period October 10, 2001 to April 4, 2002. A statistically significant increase in fluorescence and turbidity occurred between March 5, 2002 and April 4, 2002, compared to a prior "non-event" period, October 10, 2001 and January 21, 2002.

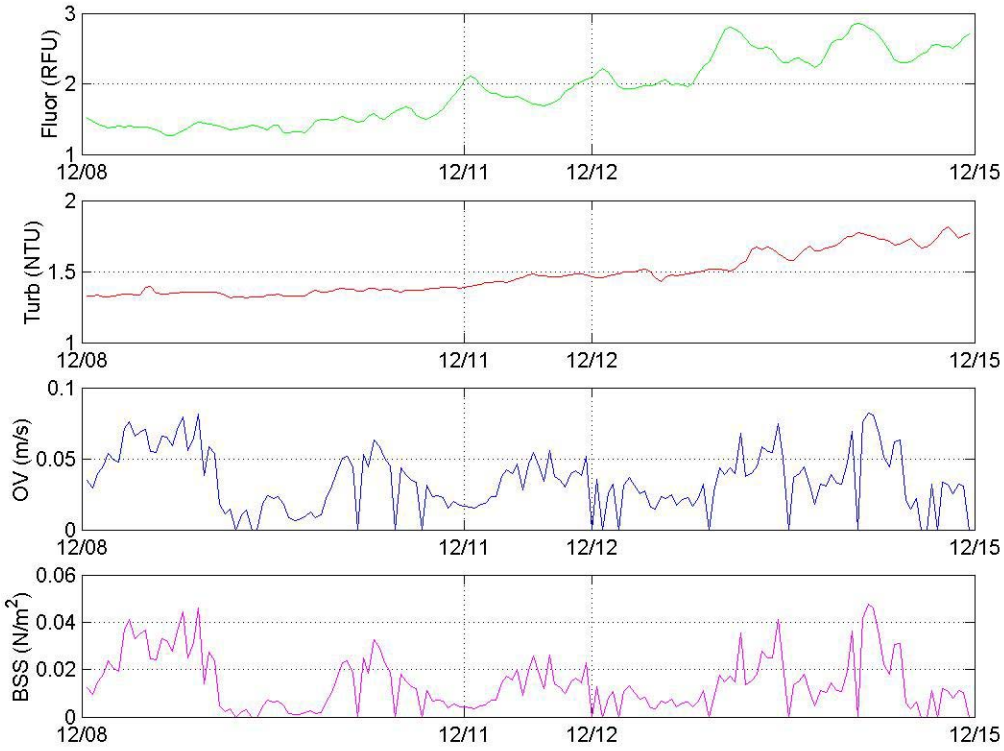

Fig.5. Plots of averaged hourly fluorescence (Fluor, RFU), turbidity (Turb, NTU), orbital velocity (OV, m/s), and bed shear stress (BSS, N/m^2) data for the period December 8, 2001 to December 15, 2001. A statistically significant increase in fluorescence and turbidity occurred between 12 and 15 of December, compared to a prior "non event" period, 8 and 11 December.

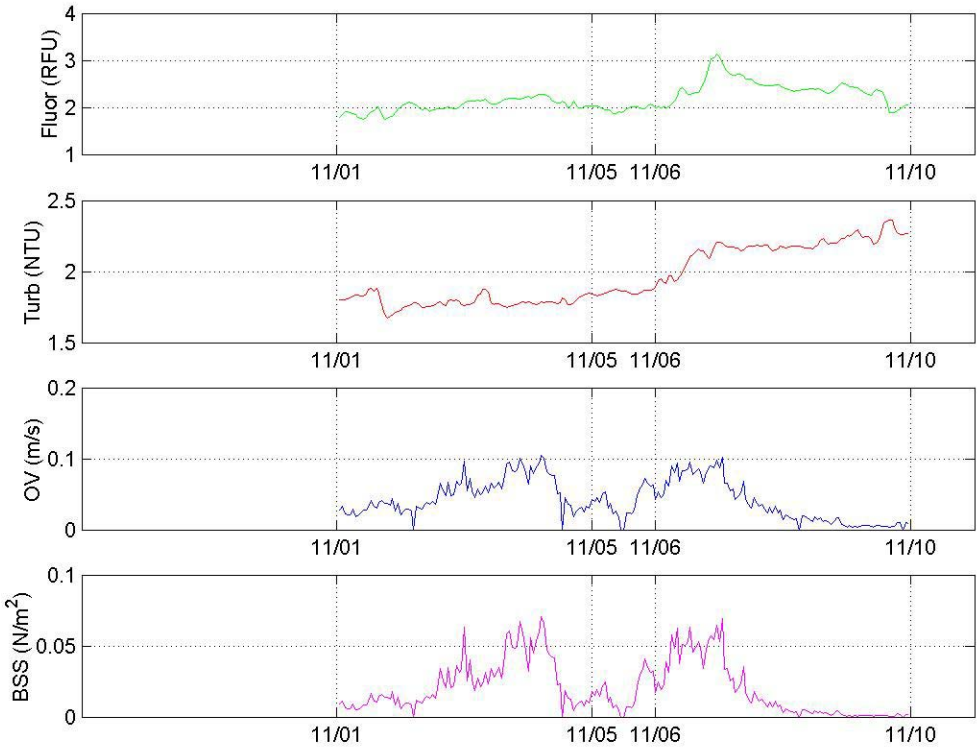

Fig.6. Plots of averaged hourly fluorescence (Fluor, RFU), turbidity (Turb, NTU), orbital velocity (OV, m/s), and bed shear stress (BSS, N/m^2) data for the period November 1, 2001 to November 10, 2001. A statistically significant increase in fluorescence and turbidity occurred between 6 and 10 of November, compared to a prior "non event" period, 1 and 5 November.

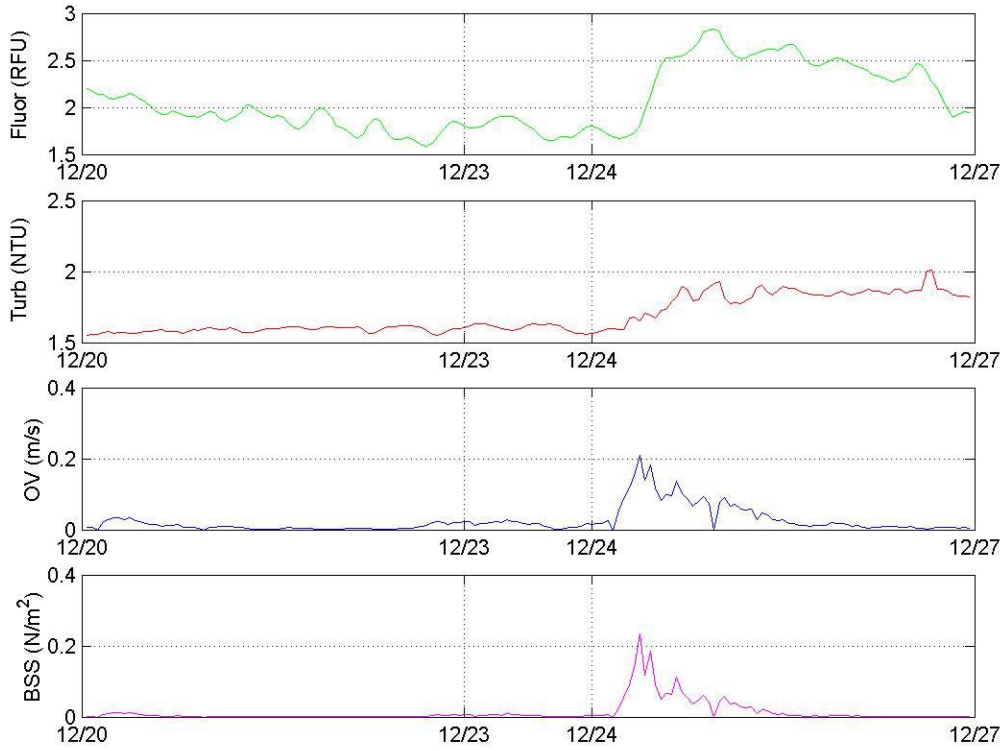

Fig. 7. Plots of averaged hourly fluorescence (Fluor, RFU), turbidity (Turb, NTU), orbital velocity (OV, m/s), and bed shear stress (BSS, N/m^2) data for the period December 20, 2001 to December 27, 2001. A statistically significant increase in orbital velocity and bed shear stress occurred between 24 and 27 of December, with concurrent significant increases in fluorescence and turbidity, compared to a prior "non event" period, 20 and 23 December.

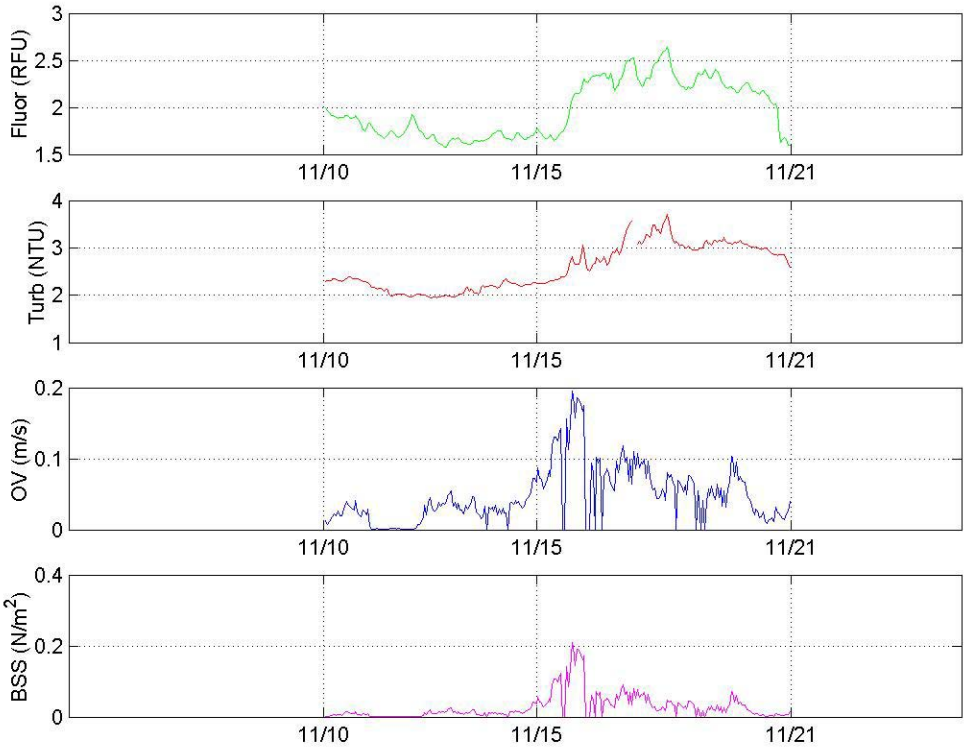

Fig.8. Plots of averaged hourly fluorescence (Fluor, RFU), turbidity (Turb, NTU), orbital velocity (OV, m/s), and bed shear stress (BSS, N/m^2) data for the period November 10, 2001 to November 21, 2001. A statistically significant increase in orbital velocity and bed shear stress occurred between 15 and 21 of November, with concurrent significant increases in fluorescence and turbidity, compared to a prior "non event" period, 10 and 15 November.

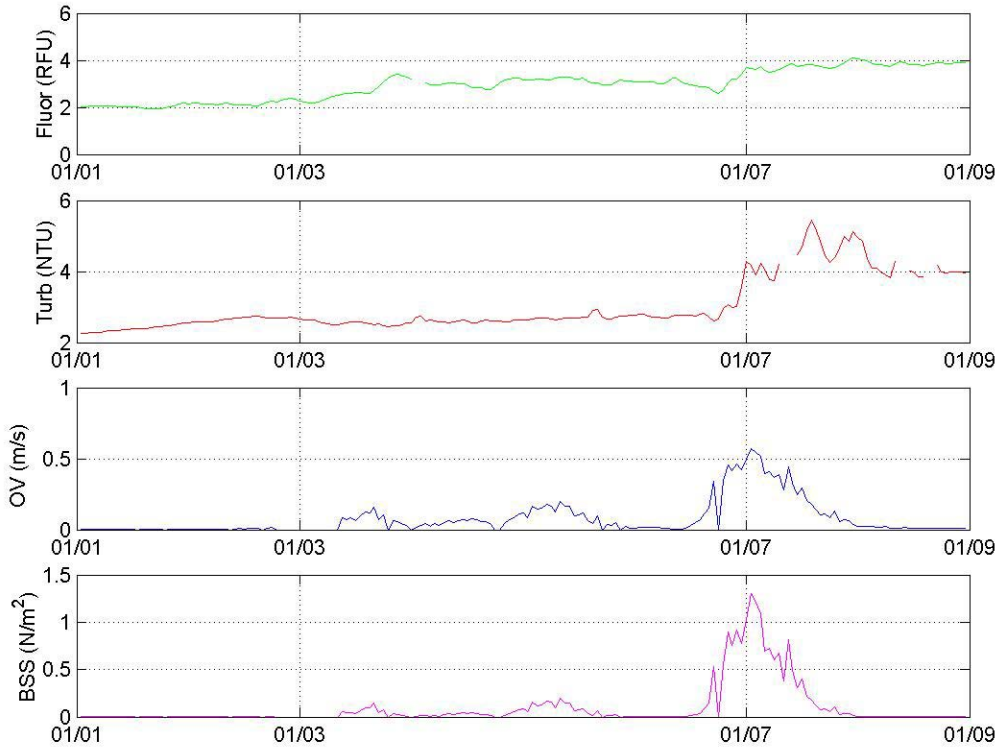

Fig. 9. Plots of averaged hourly fluorescence (Fluor, RFU), turbidity (Turb, NTU), orbital velocity (OV, m/s), and bed shear stress (BSS, N/m^2) data for the period January 1, 2002 to January 9, 2002. A statistically significant increase in orbital velocity and bed shear stress occurred between 7 and 9 of January, with concurrent significant increases in fluorescence and turbidity, compared to a prior "non event" period, 1 and 3 January.

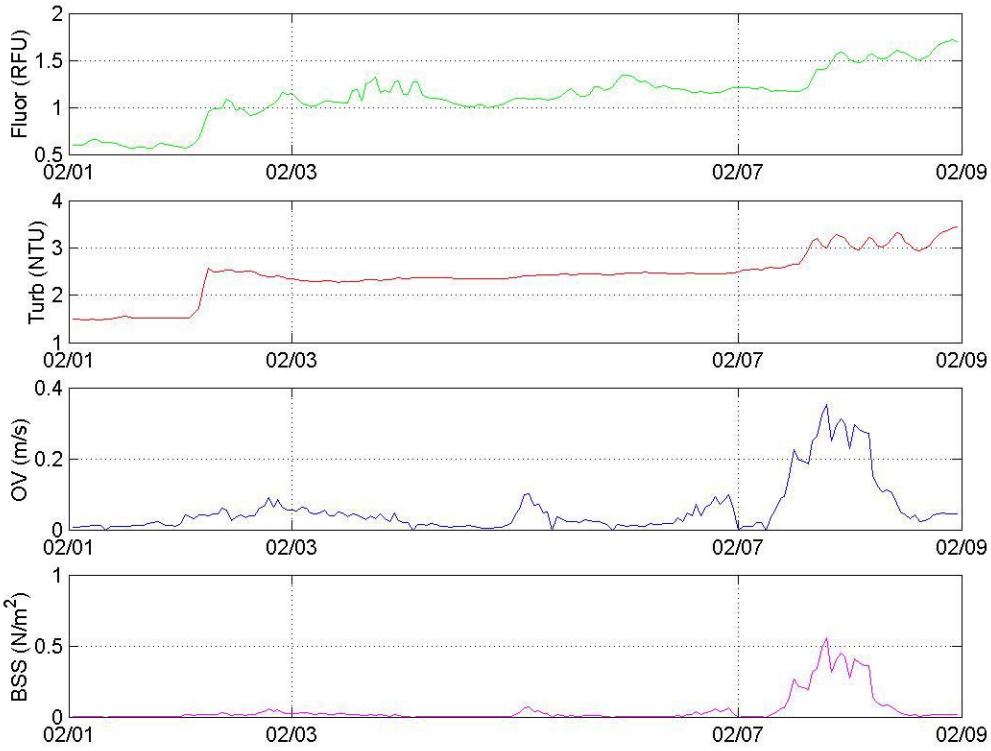

Fig.10. Plots of averaged hourly fluorescence (Fluor, RFU), turbidity (Turb, NTU), orbital velocity (OV, m/s), and bed shear stress (BSS, N/m^2) data for the period February 1, 2002 to February 9, 2002. A statistically significant increase in orbital velocity and bed shear stress occurred between 7 and 9 of February, with concurrent significant increases in fluorescence and turbidity, compared to a prior "non event" period, 1 and 3 February.

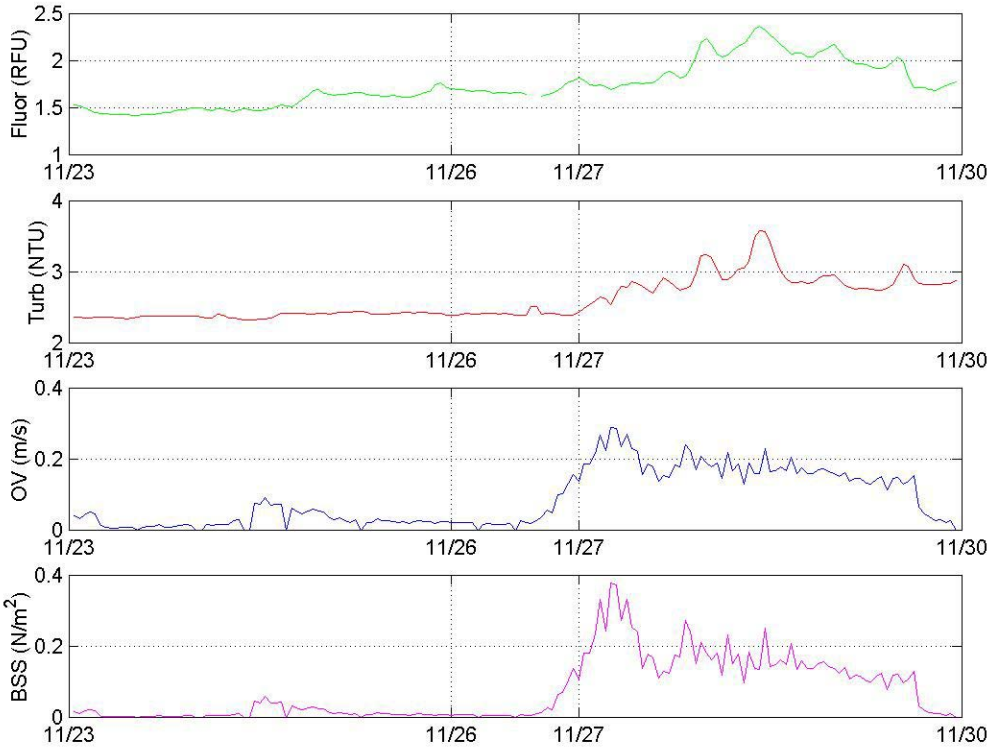

Fig.11. Plots of averaged hourly fluorescence (Fluor, RFU), turbidity (Turb, NTU), orbital velocity (OV, m/s), and bed shear stress (BSS, N/m^2) data for the period November 23, 2001 to November 30, 2001. A statistically significant increase in orbital velocity and bed shear stress occurred between 27 and 30 of November, with concurrent significant increases in fluorescence and turbidity, compared to a prior "non event" period, 23 and 26 November.

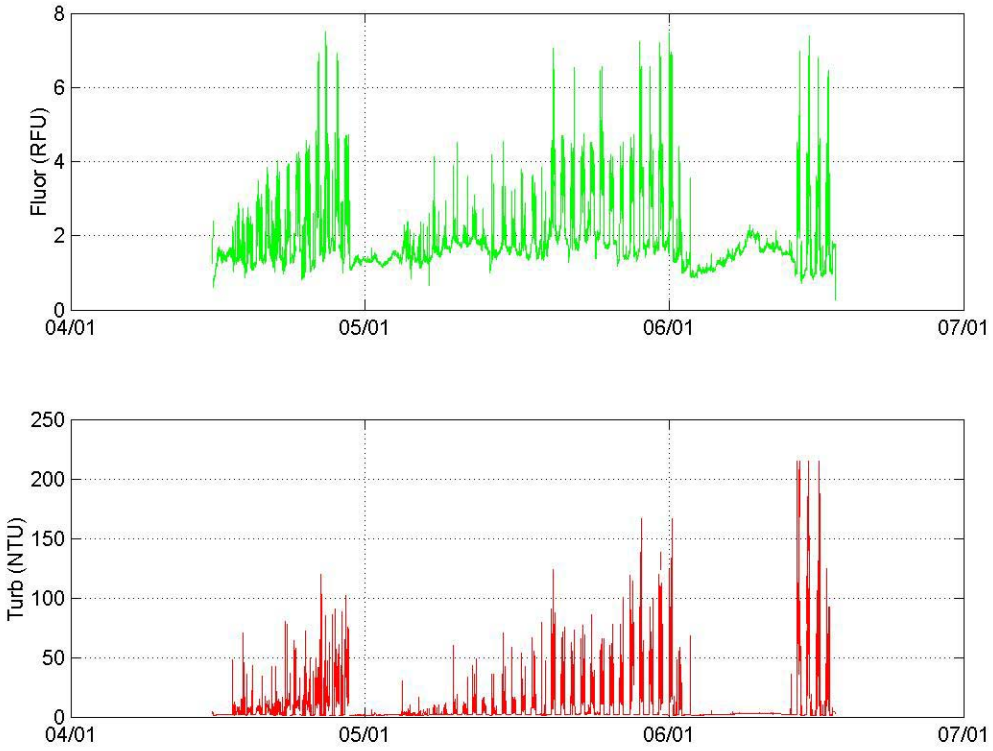

Fig.12. Plots of turbidity (Turb, NTU) and fluorescence (Fluor, RFU), at OB27 sampled every 10 minutes vs. mo/day from April 15, 2002 to June 14, 2002; SCUFA II at 1 m above the bottom.

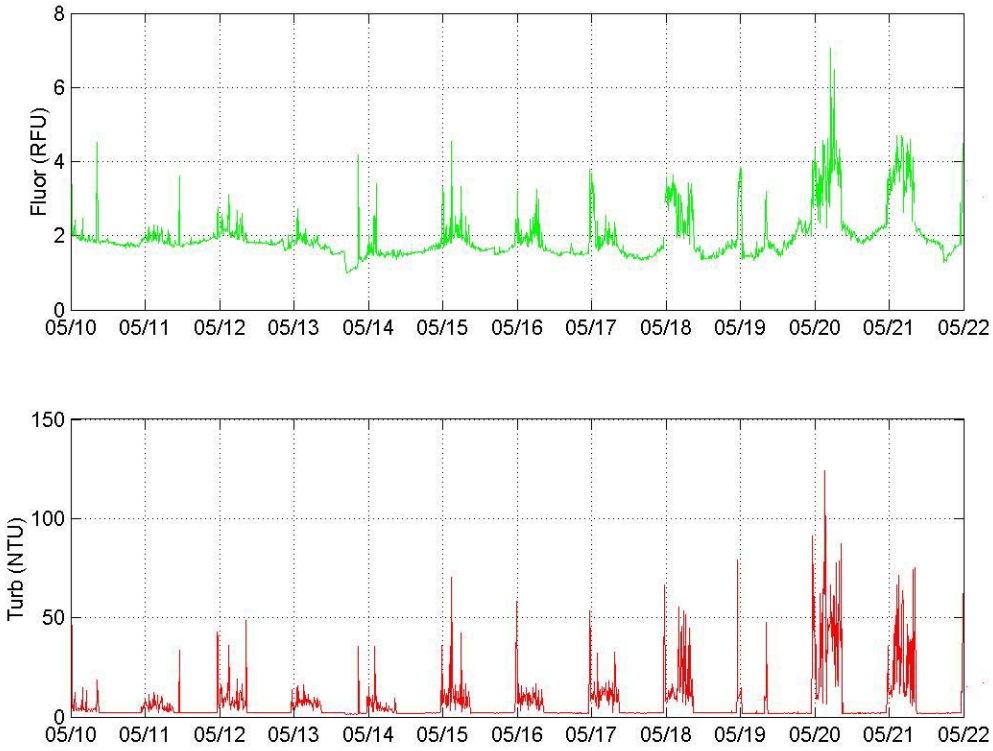

Fig.13. Plots of turbidity (Turb, NTU) and fluorescence (Fluor, RFU), at Ob27 sampled every 10 minutes from May 10, 2002 to May 22, 2002 interval steps of a day; SCUFA II at 1 m above the bottom.

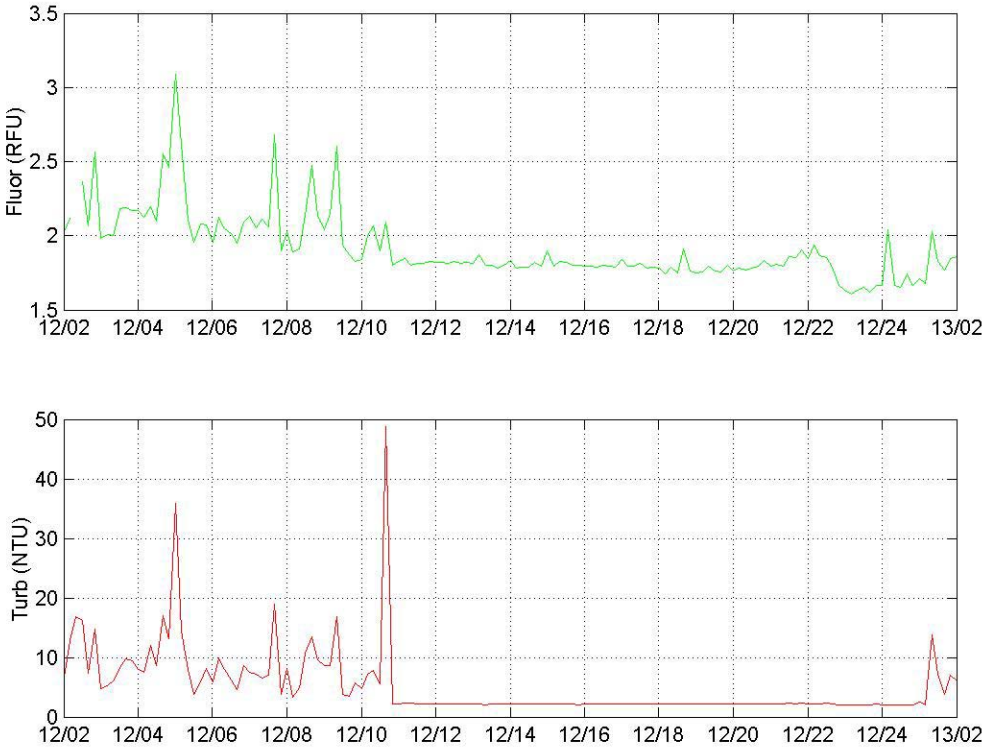

Fig.14. Plots of turbidity (Turb, NTU) and fluorescence (Fluor, RFU), at OB27 sampled every 10 minutes from May 12, 2002 tMay13, 2002 interval steps of 2 hours; SCUFA II at 1 m above the bottom.

REFERENCES

Admiraal, W., & Peletier, H. 1980. Distribution of diatoms in an estuarine mudflat and experimental analysis of the selective effect of stress. Journal of Experimental Marine Biology and Ecology 46, 157-75.

Alldredge, A.L., & King, J.M. 1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Marine Biology 41, 317-333.

Austen, I., Andersen, T.J., & Edelvang, K. 1999. The influence of benthic diatoms and invertebrates on the erodibility of an intertidal mudflat, the Danish Sea. Estuarine, Coastal and Shelf Science 49, 99-111.

Cahoon. L.B. 1999. The role of benthic microalgae in neritic ecosystems. Oceanography and Marine Biology: An Annual Review 37, 47-86.

Cahoon, L.B. & Cooke, J.E. 1992. Benthic microalgal production in Onslow Bay, North Carolina, USA. Marine Ecology Progress Series 84, 185-96.

Cahoon, L.B. 1987. The role of sediment-water column interactions in the continental shelf ecosystem. Pp 171-180, In Diving for Science….1986 (Mitchell, C., ed.) American Academy of Underwater Sciences La Jolla, CA.

Cahoon, L.B., & Laws, R.A. 1993. Benthic diatoms from the North Carolina continental shelf: inner and mid shelf. Journal of Phycology 29, 257-263.

Cahoon, L.B., Redman, R.S. & Tronzo, C.R. 1990. Benthic microalgal biomass in sediments of Onslow Bay, North Carolina. Estuarine, Coastal and Shelf Science 31, 805-16.

Curtin, T.B. 1979a. Oceanographic field observations off North Carolina. Winter survey 2-12 February, 1978. North Carolina State University Data Report, 79-3.

Curtin, T.B. 1979b. Oceanographic field observations off North Carolina. Spring survey 12-22 May, 1978. North Carolina State University Data Report, 79-4.

Curtin, T.B. 1979c. Oceanographic field observations off North Carolina. Fall survey 1-11 November, 1977. North Carolina State University Data Report, 79-5.

Decho, A.W. 1990. Microbial polymer secretions in ocean environments: their role(s) in food webs and marine processes. Oceanography and Marine Biology: An Annual Review 28, 73-153.

Hustedt, F. 1955. Marine littoral diatoms of Beaufort, North Carolina. Bulletin of the Duke University Marine Laboratory, No. 6.

Jonsson, I.G. 1975. The wave friction factor revisited: Progress Report number 37, 3-8. Institute for Hydrodynamics and Hydraulic Engineering, Technical University of Denmark, Lyngby, Denmark.

Krauss N.C. 1981. One-Line Development and Simulation for Oarai beach:Report n° 13. Nearshore Environment Research Center, Tokyo, Japan, pp. 155-192.

Laws, R.A. 1983. Preparing strewn slides for quantitative microscopical analyses: a test using calibrated microspheres. Micropaleontology 29, 60-65.

Lukatelich, R.J. & McComb, A.J. 1986. Distributions and abundance of benthic microalgae in a shallow southwestern Australian estuarine system. Marine Ecology Progress Series 27, 287-97.

McIntire, C.D., 1978. The distribution of estuarine diatoms along environmental gradients: a canonical correlation. Estuarine, Coastal and Shelf, Science 6, 447-57.

McIntire, C.D. & Moore, W.W. 1977. Marine littoral diatoms: ecological considerations. Pp 333-371, In Werner, D. (ed.) The Biology of Diatoms, Botanical Monographs, Vol. 13. University of California Press, Berkeley.

Nielson, P., 1979. Coastal bottom boundary layers and sediment transport Pp. 105-106, In Advanced Series on Ocean Engineering, Vol 4, World Scientific.

Paffenhöfer, G.-A., Diebel, D., Atkinson, L.P. & Dunstan, W.M. 1980. The relation of concentration and size distribution of suspended particulate matter to hydrography in Onslow Bay, North Carolina. Deep-Sea Research 27, 435-448.

Pietrafesa, L.J., 1978. Onslow Bay physical/dynamical experiments, summer-fall 1975: An Annual Report 78-04, Center for Marine and Coastal Studies, North Carolina State University.

Porter, J.W., & Porter, K.G . 1977. Quantitative sampling of demersal zooplankton migrating from different coral reef substrates. Limnology and Oceanography 22, 553-555.

Renaud, P.E., Stanley, R., Riggs, R., Ambrose, W.G., Schmid, K., & Snyder, S.W. 1997. Biological-geological interactions: storm effects on macroalgal communities mediated by sediment characteristics and distribution. Continental Shelf, Research 37-56.

Riethmuller, R., Haakvoort, J.H., Heineke, M., Heymann, K., Kuehl, H. & Witte, G. 2000. Relating shear stress to tidal flat surface colour. Pp 283-293, In Sedimentary Processes in the Intertidal Zone. Geological Society London, Special Publications.

Robichaux, D.M., Cohen, A.C., Reaka, M.L., & Allen, D. 1981. Experiments with zooplankton on coral reefs, or will the real demersal zooplankton please come up? P.S.Z.N.I: Marine Ecology 2, 77-94.

Roemer, S.C., Hoagland, K.D & Rosowski, J.R. 1984. Development of a freshwater periphyton community as influenced by diatom mucilages. Canadian Journal of Botany 62, 1799-1813.

Round, F.E. 1971. Benthic marine diatoms. Oceanography and Marine Biology: An Annual Review 9, 83-139.

Rowe, G. T., Clifford, C.H., Smith, K.L. Jr & Hamilton, P.C. 1975. Benthic nutrient regeneration and its coupling to primary productivity in coastal waters. Nature 255, 215-217.

Schneider, C.W. 1976. Spatial and temporal distributions of benthic marine algae on the continental shelf of the Carolinas. Bulletin of Marine Science 26, 133-151.

Shuman, F. R. & Lorenzen, C. 1975. Quantitative degradation of chlorophyll by a marine herbivore. Limnology and Oceanography 20, 580-586.

Sullivan, M. J. & Moncreiff, C.A. 1988. Primary production of edaphic algal communities in a Mississippi salt marsh. Journal of Phycology 24, 49-58.

Swart, D.H. 1974. Offshore Sediment Transport and Equilibrium Beach Profiles: Doctoral Dissertation, Department of Civil Engineering, Delft University of Technology.

Underwood, G.J.C., Paterson, D.M. & Parkes, R.J. 1995. The measurement of microbial carbohydrate exopolymers from intertidal sediments. Limnology and Oceanography 40, 1243-53.

Von Karman, T. 1930. Mechanical Similarity and Turbulence: Pp 85-92, In Proceedings of 3rd International Congress of Applied Mechanics: Volume I. Stockholm, Sweden.

Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and phaeopigments. Limnology and Oceanography 39, 1985-1993.

Whitney, D. E. & Darley, W. M. 1979. A method for the determination of chlorophyll a in samples containing degradation products. Limnology and Oceanography 24, 183-186.

Wood, R. & Widdows, J. 2002. A model of sediment transport over an intertidal transect, comparing the influences of biological and physical factors. Limnology and Oceanography 47, 848-855.

Yoder, J.A. 1985. Environmental control of phytoplankton production on the southeastern U.S. continental shelf. Pp 93-103, In Oceanography of the Southeastern U.S. Continental Shelf (Atkinson, L.P., Menzel, D.W. & Bush, K. A., eds). American Geophysical Union, Washington